A REVIEW OF THE GENUS *HALOCYNTHIA* VERRILL, 1879

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Synopsis

The genus *Halocynthia* Verrill is reduced by synonymy to six closely related species distinguished only by the condition of the gonads and the branchial and atrial spines. Considerable variation in external appearance is demonstrated within a single species.

Species occur in the littoral fringe of land masses and generally have a wide latitudinal range. Their distribution appears to be limited mainly by deep waters. The genus appears to be an ancient one and it may represent a relict of the Tethys Sea fauna.

INTRODUCTION

The genus *Halocynthia* Verrill, is an homogeneous one, comprising only a limited number of closely related species. These generally have a wide cosmopolitan distribution from north to south along the sub-littoral fringe of land masses in depths up to about 200 m. Geographic isolation is not always a major factor in speciation and phylogeny of the genus is discussed. An attempt is made in the present work to define the limits of intraspecific variation and to clarify the taxonomy of the genus.

Genus HALOCYNTHIA Verrill, 1879

Type Species.—Ascidia papillosa Linnaeus, 1767.

Test produced into spines. Longitudinal glandular plications and arborescent liver lobes present in the pyloric region. Gonads form, on each side of the body, a parallel series of tubular ovaries surrounded by testis lobes, each gonad terminating in a ♀ and ♂ duct directed toward the atrial opening. On the left the gonads are in the gut loop and the ducts extend across the descending limb of the intestine. A double series of languets present along the dorsal line.

Species of this genus are present in sand, gravel or on rocks but never in mud. The genus has been recorded, on several occasions, with the phanerogam, *Posidonia*, which also flourishes on a sandy substrate (*H. papillosa* in the Mediterranean and *H. hispida* in South Australia). Further, the genus is invariably taken in fairly shallow water (up to 200 m. but generally less) in sheltered waterways and estuaries where terrestrial run-off and/or melting ice might be expected to affect the salinity of the water, e.g., Upper St. Vincent's Gulf, Port Jackson, D'Entrecasteaux Channel, Akkeshi Bay, Puget Sound, Massachusetts Bay, Gulf of St. Lawrence, Iceland, Greenland, etc.

Key to the Species of Halocynthia

1	Spines around apertures with secondary spines	2
	Spines around apertures without secondary spines	4
2(1)	1 or 2 gonads per side, not parallel, no spinules on shaft of spines	*H. igaguri* Tokioka (Inland Sea, Japan)
	Spinules on shaft of spines	3

3(2) More than 2 parallel gonads per side ..... *H. hispida* (Herdman)
(Hokkaido, Ceylon, East Australia and South Australia)
2 parallel gonads joining ventrally to form a U ..... *H. spinosa* Sluiter
(South Africa, East Africa, Red Sea)

4(1) 2 parallel gonads joining ventrally to form a U ..... *H. papillosa* (Linnaeus)
(Mediterranean, Adriatic)
More than 2 parallel gonads joined ventrally 5

5(4) Surface of test raised into small spine bearing elevations (*H. aurantium* (Pallas)) 6
Surface of test not raised into small spine bearing elevations *H. roretzi* (Drasche)
(Northern Japan, Japan Sea)

6(5) North Pacific ..... *H. aurantium* sub. sp. *typicum*
North Atlantic ..... *H. aurantium* sub. sp. *pyriformis*

Halocynthia hispida (Herdman, 1881)

(Text-fig. 1)

Cynthia hispida Herdman, 1881, p. 61; 1882, p. 146; *Cynthia crinitistellata* Herdman, 1899, p. 34; 1906, p. 313; *Halocynthia hispida*; Kott, 1952, p. 283 var. *typica*; 1952, p. 284 var. *crinitistellata*; 1954, p. 129 var. *crinitistellata*; *Cynthia hilgendorfi* Traustedt, 1885, p. 36; Oka, 1935, p. 436; *Halocynthia hilgendorfi*; Hartmeyer, 1906, p. 6; Tokioka, 1959, p. 233; f. *ritteri*, 1962, p. 18; *Halocynthia owstoni* Oka, 1906, p. 42; *Halocynthia ritteri* Oka, 1906, p. 43; *Halocynthia igaboja* Oka, 1906, p. 45; Van Name, 1945, p. 362; *Halocynthia okai* Ritter, 1907, p. 11; Ritter and Forsyth, 1917, p. 441; *Pyura okai;* Hartmeyer, 1909-11, p. 134; *Tethyum igaboja* Huntsman, 1912, pp. 114, 115, 136; Van Name, 1945, p. 362; *Cynthia pachyderma* Oka, 1926, p. 559; *Cynthia cactus* Oka, 1932, p. 131; *Halocynthia cactus;* Tokioka, 1953, p. 285; Rho, 1966, p. 213; 1966*a*, p. 366; ? *Halocynthia simaensis* Tokioka, 1949, p. 62.

Description.—The body is rounded, maximum diameter from 3 to 10 cm. Individuals are often crowded together and the body becomes misshapen. The colour is always red-orange. Posteriorly the test is produced into irregular root-like processes. The test may be fairly thick and is always tough and very leathery externally. The surface of the body is even; or produced into tubercular prominences which are evenly distributed about 5 mm. apart over the whole surface, or irregularly distributed. These tubercular prominences are especially noticeable in the siphonal region where they are best developed. Generally there seems to be a tendency to loss of the tubercular prominences on the body with an increase in size although they do persist in the siphonal region. There is also a tendency for the surface of the body to become increasingly rough and wrinkled with increasing size.

Long spines of 2 to 3 mm. or more are often present either distributed evenly over the body surface (*C. cactus* Oka, 1936); or supported by the tubercular prominences singly or in groups of 2 to 3 (*C. crinitistellata* Herdman, 1899; Kott, 1952; *C. hilgendorfi*; Oka 1935; *H. igaboja* Oka, 1906; Van Name, 1945). These long spines are absent altogether from some specimens (*C. hispida* Herdman, 1882; Kott, 1952. H. *ritteri* Oka, 1906; Tokioka, 1962). In the present collection from St. Vincent's Gulf all varieties of test spine development are present:

Carickalinga Heads, 20 to 15 ft., "in caves and on vertical rock faces":

(1) Even surface, globular body with slightly protruberant siphons. Only few inconspicuous longer spinous processes from the test. Smaller test spines covering the surface consist of 6 to 8 long radiating processes and a single terminal process. Single specimen.

(2) Thickly distributed long spinous processes over the surface, longer anteriorly, these are not always supported by tubercular prominences. Small test spines covering the surface. Single specimen.

Off Port Stanvac, on steel wreckage:

Surface uneven, rounded tubercular prominences especially anteriorly, supporting single median, or several long spines. Smaller test spines with 6 to 8 stiff radiating processes. Single specimen.

St. Vincent's Gulf, Posidonia beds:

Surface generally uneven with tubercular prominences, or irregular transverse wrinkles. Long spinous processes present all over the body or confined to the region around the siphons. Smaller test spines with 6 to 8 stiff radiating processes. Numerous specimens.

No constant condition in the distribution of the spines and tubercular prominences has been observed in the specimens from any one area which would suggest geographical subspecies: and specimens with spine arrangement intermediate between those types described above are constantly encountered. It is possible that the differences reflect to some extent environmental factors (see below). Spines sometimes increase in length anteriorly and in larger specimens become leathery. They have secondary spines terminally and in 2 to 3 concentric rings along the shaft. The secondary spines tend to lose their concentric arrangement as the spines become more leathery and their distribution consequently becomes less regular. The shafts of the spines are covered by regularly spaced minute spinules.

Over the whole surface of the test, between the longer spines, minute, almost confluent papillae support 6 to 8 radiating spines or processes; or they occasionally terminate in a single spine. The surface of these papillae is also covered with spinules as on the shaft of the longer spines. These papillae and the processes they support give to the surface of the test a downy appearance. Always present around the apertures is a circle or thicket of larger spines sometimes branched, and similar to those found elsewhere on the test in the majority of specimens. They have secondary spines terminally and in concentric circles along the shaft and they have spinules on the shaft.

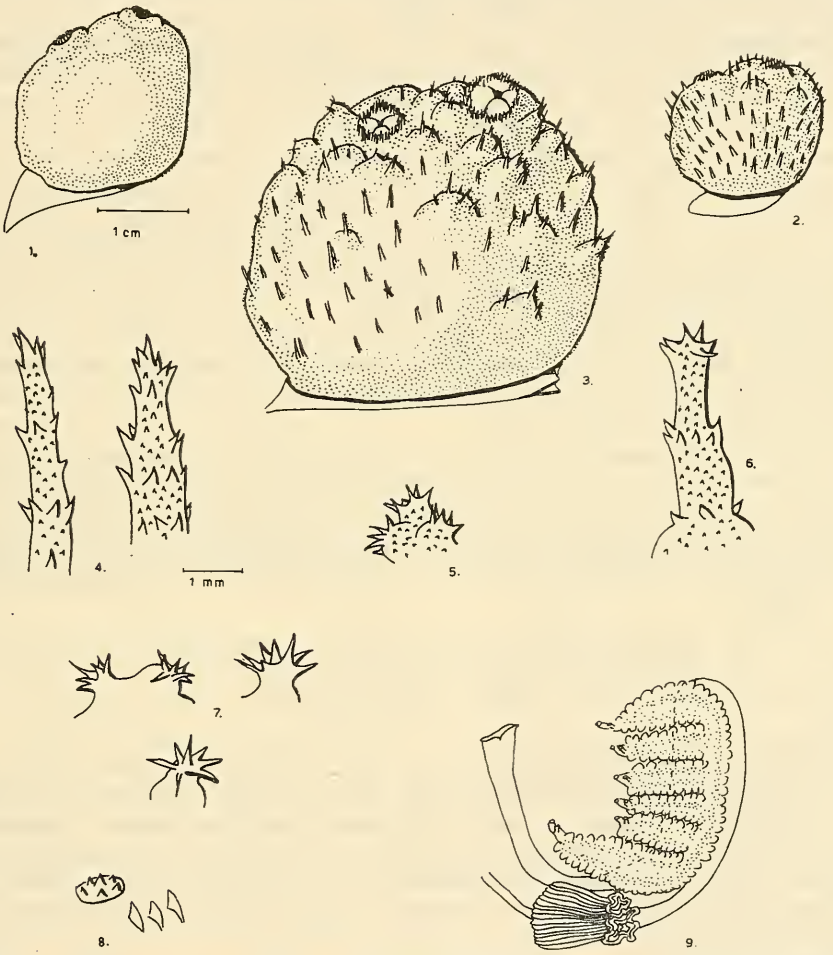
In the siphon linings scale-like swellings continuous with the small spine bearing papillae of the test extend in a single row down the folds which correspond to the branchial and atrial lobes. These support one or more small spines and in the furrows between the folds are reduced to single conical spines or papillae.

Branchial tentacles vary from 8 to 16 with well-developed primary branches supporting a fringe of minute secondary branches. Dorsal tubercle forms a double spiral cone and rarely deviates from this condition. Dorsal lamina consists of a row of pointed languets, closely placed; and to the right of this a second row of similar languets but not so closely placed. The branchial sac has 9 to 10 folds on each side of the body. The most central fold on each side is often rudimentary. The maximum number of vessels on a single fold is from 18 in a specimen of 1·8 cm. high up to 25 to 37 in specimens greater than 5 cm. There are from 1 to 3 longitudinal vessels between the folds. Stigmata per mesh vary from 4 to 10 in individuals of 2 to 7 cm. *H. cactus*; Tokioka, 1953, 8 cm. high had 20 to 23 stigmata in the largest meshes but Oka's specimens from the same locality and otherwise identical with the former have a smaller number of stigmata in each mesh.

The gut loop is simple and closed. The ascending rectum extends anteriorly to terminate in a smooth rimmed anus. Anterior glandular

plications are present in the pyloric region and distal to these a collection of arborescent liver lobules form a half ring around the gut usually on its mesial surface. However, these may be displaced anteriorly around the intestine.

Gonads vary from 2 to 10 parallel ovarian tubes on each side of the body, directed toward the atrial opening. They are joined ventrally by an antero-posteriorly oriented connective. Testes lobes are arranged along both sides of the ovaries and in mature specimens extend as a continuous mat



Text-figure 1.—*Halocynthia hispida* (from St. Vincent's Gulf). 1 and 2. Specimens from Carickalinga Heads; 3. Specimen from Posidonia beds; 4. Spines from thicket around apertures; 5. Small spines on lobes of apertures; 6. Long test spine; 7. Small test spines evenly distributed over surface; 8. Spines from inner lining of apertures; 9. Diagram of gut and gonads on the left.

between and on the parietal side of the ovaries. Testes ducts join on the surface of each ovarian tube and form a vas deferens to open adjacent to the oviduct. Occasionally gonads are missing or reduced on the right side of the body. On the left they are present in the gut loop.

New Records.—From Posidonia beds, St. Vincent's Gulf, South Australia, 5 fm.; 4 mls off Pt. Stanvac, South Australia, on steel wreckage, 15 fm.

Carickalinga Heads, 15 to 20 ft. in caves and on vertical rock faces, South Australia. Coll. S. A. Shepherd.

Previous Records.—D'Entrecasteaux Channel, Tasmania, 5 fm. (Kott, 1952); off Maria Island, Tasmania, 174–155 m., 676–128 m. (Kott, 1954); Bass Strait, 38–40 fm. (Herdman, 1882); Port Jackson (Herdman, 1899; Kott, 1952); Ceylon, 6–9 fm. (Herdman, 1906); Hokkaido, Japan (Traustedt, 1885; Oka, 1906); Honshu, Kyushu, Japan (Oka, 1906, 1932, 1935; Tokioka, 1949, 1953, 1959, 1962); British Columbia to California, 10–90 fm. (Ritter, 1907; Huntsman, 1912, 1921; Van Name, 1945).

Distribution.—In 5–90 fm. in the Pacific Ocean from Hokkaido to southern Australia in the west and from British Columbia to California in the east. The species has not been recorded from New Zealand; nor from any other islands in the Pacific and its spread may be limited by deeper waters. Records are lacking from the Malayan Peninsula, Indonesia, west and north-east Australia. Further collecting may establish some continuity between the Japanese, Ceylon and Australian specimens as there is no morphologically stable characters which might suggest isolated communities in these areas. Nor is its recorded distribution continuous across the north Pacific Ocean from Hokkaido to British Columbia.

Habitat.—Van Name (1945) describes the species as present on a sandy or gravelly bottom. The present specimens are described as "thick in Posidonia beds"; "vertical rock faces". Specimens from d'Entrecasteaux Channel were from scallop beds.

Remarks.—Externally therefore specimens of this species vary in external appearance and may be characterised as belonging to the following types:

(*a*) Long spines absent from body of the individual; surface even: *Cynthia hispida*, Herdman, 1882, Bass Strait; *Halocynthia hispida* var. *typica* Kott, 1952, d'Entrecasteaux Channel; *Halocynthia ritteri* Oka, 1906; Tokioka, 1962, Japan.

(*b*) Long spines randomly distributed over the body of the individual; surface even: *Halocynthia cactus* Oka, 1932; Tokioka, 1953, Sagami Bay, Japan; *Halocynthia igaboja* Oka, 1906; Van Name, 1945, Japan and East Pacific.

(*c*) Some spines present on parts of the body (intermediate between (*a*) and (*b*)): *Cynthia hilgendorfi* Traustedt, 1885; f. *ritteri* Tokioka, 1959, Japan.

(*d*) Surface of body raised into tubercular prominences supporting longer spines: *Cynthia crinitistellata* Herdman, 1899; Herdman, 1906, Port Jackson, Ceylon; *Halocynthia hispida* var. *crinitistellata* Kott, 1952, Port Jackson; Kott, 1954, off Maria Island, Tasmania; *Halocynthia hilgendorfi*; Oka, 1935, Japan.

It has not been possible to divide specimens demonstrating these various conditions of the test into geographical sub-species. However, it is possible that the variations occur in response to some environmental factor.

The species resembles *H. spinosa* Sluiter in the form of the longer spines on the test; however, in the latter species the smaller spines which cover the test and cause its granular consistency are supported on small scale-like areas rather than papillae, similar to the condition in *H. aurantium* but distinct from the homologous structures in *H. hispida*. *Cynthia crinitistellata* Herdman, 1906 from Ceylon has papillae rather than scales supporting the test spines and despite its location geographically is undoubtedly a synonym of *H. hispida*.

H. simaensis Tokioka is listed as a doubtful synonym of this species. Although externally the specimen resembles larger specimens of the present species the glandular plications of the pyloric region are subdivided into lobes; and spines are absent from the siphonal lining. So far only a single specimen is known. Further collection may confirm these characters as indicating specific distinctions rather than individual abnormality or the effects of age. The absence of gonads on the right is not necessarily significant as the number of gonads, especially on the right, varies considerably.

Herdman (1899) considers *Cynthia dumosa* Stimpson, 1855, a very likely synonym of the present species. However, Stimpson's specimen was not the characteristic orange-red colour of *H. hispida*; and was taken from Port Jackson on a muddy substrate which is unusual for *H. hispida*.

Halocynthia aurantium (Pallas, 1787)

(Text-fig. 2, (10-12))

Ascidia aurantium Pallas, 1787, p. 24. (For further synonymy see accounts of subspecies below.)

Description.—Halocynthia aurantium (Pallas, 1787) from the north Pacific and *H. pyriformis* (Rathke, 1806) from the north Atlantic both have papillary swellings all over the test supporting pointed spines singly or in groups. The spines, however, do not radiate as in *H. hispida* but are shorter, project forwards, and have a central spine which is longer than those which surround it. The species lacks the longer branched spines of *H. hispida* although a circle of enlarged spines is present around the apertures with minute spinules or barbs along the shaft. Other characters resemble those in *H. hispida*. The two subspecies are distinguished from one another only by the numbers of gonads on each side of the body: 3 to 7 for sub. sp. *pyriformis* and 3 to 4 for sub. sp. *aurantium*. This, as observed by Van Name (1945) and Arnbäck (1928) does not constitute a very convincing distinction and relationships are better indicated by subspecific than by specific rank.

Halocynthia aurantium (Pallas, 1787)
sub. sp. *typica*

(Text-fig. 2, (11-12))

Ascidia aurantium Pallas, 1787, p. 240; *Cynthia pyriformis*; Traustedt, 1885, p. 34 (part); *Cynthia superba* Ritter, 1900, p. 590; Pratt, 1916, p. 667; *Cynthia deani* Ritter, 1900, p. 590; *Halocynthia superba*; Oka, 1906, p. 41; Hartmeyer, 1903, p. 200; *Halocynthia deani;* Hartmeyer, 1903, p. 200; *Tethyum aurantium*; Huntsman, 1912, pp. 114, 115, 136; 1912*a*, p. 173; Redikorzev, 1916, p. 169 (part); *Halocynthia aurantium*; (part) + *forma koreana* Hartmeyer, 1903, pp. 195, 200; *Halocynthia aurantium*; Ritter, 1913, p. 448; + *H. superba* Michaelsen, 1919, p. 11; Hartmeyer, 1921, pp. 30, 33; Arnbäck 1928, p. 84; Pratt, 1935, p. 748; Van Name, 1945, p. 362; Tokioka, 1951, p. 17; 1967, p. 219; Monniot, 1965, p. 115.

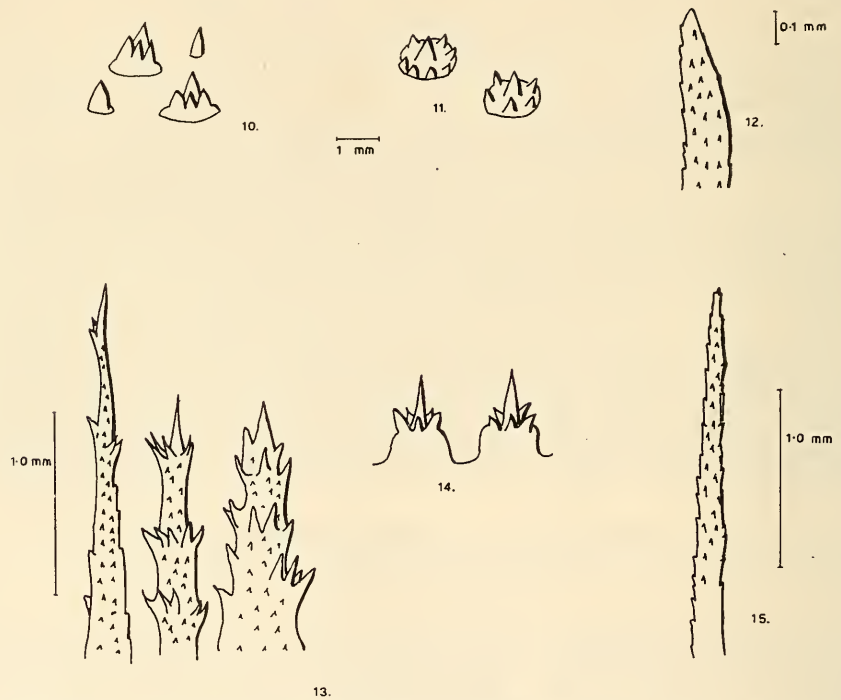
Records.— Korea (Hartmeyer, 1903); Hokkaido (Traustedt, 1885; Oka, 1906; Tokioka, 1951, 1966); Kuril Is. (Pallas, 1787); Vladivostok, Okhotsok Sea (Redikorzev, 1916); Bering Sea, Bering Straits, Puget Sound (Huntsman, 1912, 1912*a*; Ritter, 1900, 1913); Alaska, Pribilof Islands (Ritter, 1913).

Distribution.—A continuous distribution is recorded from the Bering Sea to overlap limits of *H. hispida* off Hokkaido and Korea in the north-western Pacific and off north-west America south to Puget Sound.

Habitat.—The subspecies is taken in waters from 10 to 180 m. on sand, sand with stones and shells, and sometimes on rocks (Arnbäck, 1928).

HALOCYNTHIA AURANTIUM (Pallas, 1787)
sub. sp. *pyriformis* (Rathke, 1806)
(Text-fig. 10)

Ascidia pyriformis Rathke, 1806, p. 41; Sars, 1851; *Cynthia papillosa*; (part) Traustedt, 1880, p. 407; Non Gunnerus, 1765; *Cynthia pyriformis*: Stimpson, 1854, p. 20; 1860, p. 1; Packard, 1863, p. 412; Binney, 1870, p. 17; Dall, 1870, p. 255; 1872, p. 157; Morse, 1871, p. 352; Kiaer, 1893, p. 67; 1896, p. 12; Metcalf, 1900, p. 510; Hartmeyer, 1901, p. 49; 1915, p. 313, *Rhabdocynthia pyriformis*; Verrill, 1879, p. 27; Whiteaves, 1901, p. 268; Michaelsen, 1918, p. 11; Hartmeyer, 1920, p. 127; 1921, p. 30; 1923, p. 163; Arnbäck, 1928, p. 33; Pratt, 1935, p. 748; Van Name, 1945, p. 359; Millar, 1966, p. 99;



Text-figure 2.—*Halocynthia aurantium* subsp. *pyriformis* (after Millar, 1966). 10. Small test spines. *Halocynthia aurantium* subsp. *typica* (after Tokioka, 1951). 11. Small test spine; 12. Spine from thicket around apertures. *Halocynthia spinosa*. 13. Spines from around apertures (after Michaelsen, 1918); 14. Small test spines (after Millar, 1962). *Halocynthia papillosa* (after Michaelsen, 1918). 15. Spine from around apertures.

Tethyum pyriforme; Hartmeyer, 1914, p. 1103; Berrill, 1935, p. 257; *Tethyum pyriforme americanum* Huntsman, 1912, pp. 112, 148; Berrill, 1929, pp. 46, 48; 1935, p. 269; *Pyura pyriformis*; Procter, 1933, p. 284; *Cynthia nordenskjoldi* Wagner, 1885, p. 156; Herdman, 1891, p. 577; *Cynthia papillosa*; Jacobson, 1892, p. 156; *Halocynthia arantium*; Hartmeyer, 1903, p. 195 (part); Bjerkan, 1908 (part); Michaelsen, 1918, p. 11; Harant, 1929, p. 66; *Pyura aurantium*; Hartmeyer, 1909–11, p. 1331; Van Name, 1912, p. 532; *Tethyum aurantium*; Redikorzev, 1916, p. 169; *Pyura pectinicola* Michaelsen, 1908, p. 262; Hartmeyer, 1909–1911, p. 1341; *Tethyum microspinosum* Van Name, 1921, p. 443.

Records.—Massachusetts Bay, Gulf of St. Lawrence, Labrador (Van Name, 1912, Huntsman, 1912); Ellesmeere Land, west coast of Greenland, Iceland (Traustedt, 1880, Arnbäck, 1928); Faroe Is., Spitzbergen, Barents Sea (Redikorzev, 1916, Arnbäck, 1926); north-western Norway (Arnbäck, 1928, Millar, 1966); Bergen (Rathke, 1906, Hartmeyer, 1901, 1923) White Sea; Murman coast (Redikorzev, 1916).

Distribution.—A continuous distribution across the north Atlantic with its most southern extent at Bergen in the east and Massachusetts in the west. In the north it extends from Ellesmeere Land the west coast of Greenland, Iceland, the Faroe Is., Spitzbergen and the Barents Sea. It is therefore present much further to the north than *H. aurantium* sub. sp. *typica* of which the most northern limit is the Bering Straits. There are no records from further east than the White Sea.

Habitat.—The species is taken from rock, sand, stones and shell in waters of 0 to 114 m.

Halocynthia spinosa Sluiter, 1905

(Text-fig 2, (13, 14))

"An *Ascidia quadridentata* L." Forskal, 1776, p. 9; *Halocynthia spinosa* Sluiter, 1905, p. 16; Michaelsen, 1918, p. 7; *Pyura spinosa*; Hartmeyer, 1909, p. 1341; *Pyura (Halocynthia) spinosa*; Hartmeyer, 1912, p. 181; *Halocynthia spinosa* f. *defectiva* Millar, 1962, p. 201; *Halocynthia arabica* Monniot, 1965, p. 121; f. *defectiva*; Monniot, 1965, p. 121; ? *Halocynthia* sp. Harant, 1929, p. 67.

Description.—In this species the longer spines on the body and in a thicket around the apertures are similar to those of *H. hispida*, with terminal secondary spines and secondary spines more or less in concentric rings along the shaft. Spinules are also present on the shaft of these spines. However, the species is distinguished by the U-shaped gonads on each side of the body similar to the gonads of *H. papillosa*; and by the distribution and form of the small test spines, supported on scale-like thickenings of the test 0·5 mm. in diameter and consisting of a central spine 0·5 mm. long surrounded by 5 to 6 smaller spines 0·25 mm. long distributed around the border of the scale. These minute test spines are also similar to those of *H. papillosa*.

Records.—Red Sea, Gulf of Aden (Michaelsen, 1918); Somaliland (Sluiter, 1905); Cape Province, South Africa, 0—13 m. (Millar, 1962); ? West of Gibraltar, eastern Atlantic, 3745 m. (Harant, 1929).

Habitat.—The specimens from South Africa were all taken from rock. There is no information on the type of substrate from which specimens from other localities were taken.

Remarks.—Millar's f. *defectiva*, taken from three different locations between January and March, was so named due to the absence of gonads on the right side of the body. While in Michaelsen's specimens of the present species gonads were absent on the right side. This absence of gonads from one side occasionally occurs in other species of this genus but its significance is not apparent.

The small specimen taken from 3745 m. west of Gibraltar (Harant, 1929) has test spines typical of the present species, and, although the gonads are not developed, probably represents an individual of this species. There are no other records of *H. spinosa* from the Atlantic coast of Africa and this single specimen may represent a relict population in deeper water.

The derivation of *H. spinosa* from the Mediterranean species *H. papillosa* by the development of secondary spines on the longer spines of the test is

suggested by their otherwise close morphological similarity. Spread of the ancestral species is unlikely through the Suez area as no continuity of the marine environment existed there previous to the opening of the Suez canal in the nineteenth century. *Halocynthia papillosa* has been known from the Mediterranean since the seventeenth century and Forskal's report of an *Ascidia quadridentata* (synonym of *H. spinosa*) is from the Red Sea in the eighteenth century. The presence of *H. spinosa* in eastern Atlantic as indicated by Harant's (1929) specimen suggests a (not necessarily contemporary) circum African distribution for the species. It is therefore most likely that the ancestral species was continuous from the western Mediterranean and around via South Africa to the Red Sea. The Straits of Gibraltar subsequently provided a sufficient barrier for the isolation of two distinct populations representing the species *H. spinosa* and *H. papillosa*.

The significance of the close morphological relationship between this species and *H. hispida* is also puzzling. In view of the wide distribution of this and other species of the genus, there is no apparent isolating barrier between *H. hispida* from Ceylon (Herdman, 1906) and the present species from the Red Sea. The relationships of these and other species of the genus are indicated in Text-fig. 3 and Table 1.

Halocynthia papillosa (Linnaeus, 1767)
(Text-fig. 2 (15))

Ascidia papillosa Linnaeus, 1767, p. 1087; *Tethyum papillosum* Gunnerus, 1765, p. 100; *Cynthia papillosa*; Savigny, 1816, p. 143; Heller, 1877, p. 249; Lacaze Duthiers and Délage, 1892, p. 126; Roule, 1885, p. 180; Herdman, 1891, p. 576; *Halocynthia papillosa*; Hartmeyer, 1904, p. 322; Michaelsen, 1918, p. 10; Harant, 1929, p. 66; Harant and Vernieres, 1933, p. 24; Pérès, 1958, p. 161; Monniot, 1965, p. 113; *Pyura papillosa*; Hartmeyer, 1909, p. 1340; 1912, p. 181; *Ascidia rustica* Risso, 1826, p. 274; non Linné, 1772.

Description.—This species closely resembles *H. aurantium* in the distribution and form of the small test spines, and in the distribution and form of the larger spines which are present around the siphons. The larger spines lack secondary spines but have spinules. However, the species are distinguished by the U-shaped gonads of *H. papillosa*.

Records.—Western Mediterranean (Pérès, 1958, Harant and Vernieres, 1933); Adriatic (Heller, 1877); Atlantic coast of France (Harant and Vernieres, 1933, Lacaze Duthier and Délage, 1892).

Habitat.—From amongst coralline algae, *Posidonia* sp., sand and shell.

Remarks.—The morphological relationships between the present species and *H. aurantium* in the north Atlantic and *H. spinosa* in the Red Sea are indicated in Table 1.

Halocynthia igaguri Tokioka, 1953

Halocynthia igaguri Tokioka, 1953, p. 20.

Description.—This species is distinguished from all others by the gonads which appear to be of a simple styelid type with tubular oviduct surrounded by pyriform testes lobes. The long spines on the test have secondary spines but no spinules and between these there are minute papillae evidently without terminal spines as in *H. hispida, H. aurantium* and *H. papillosa*. There are only 7 branchial folds per side and Tokioka has not described a double series of languets along the dorsal line.

Record.—Inland Sea, Japan (Tokioka, 1953).

Remarks.—The condition of the gonads, number of branchial folds and the dorsal lamina are not typical of this genus. However, there are the usual glandular plications and liver lobes in the pyloric region.

Halocynthia roretzii (Drasche, 1884)

(*Styela?*) *Cynthia roretzii* Drasche, 1884, p. 376. For further synonymy see Tokioka, 1953, p. 282.

Description.—Specimens are up to 14 cm. long. This species has circles of spines around the apertures similar to those of *H. aurantium* with spinules but no secondary spines. The surface of the test is divided into scale-like areas without spines, as in *H. aurantium.* In older specimens large mammillary or finger-like processes develop from the test sometimes bearing a terminal spine. There are very numerous branchial folds—up to 18 on each side with 60 to 70 longitudinal vessels on each fold. Gonads are numerous—7 to 11.

Younger specimens have neither mammillary nor finger-like processes and no polygonad scale-like areas; the surface has instead a number of spines with spinules similar to those present around the apertures of the adult.

Table 1

Morphological relationships between common species of the genus Halocynthia

		Gonads	
		U-shaped gonads	Many parallel gonads
Secondary spines on Test spines	Absent	*H. papillosa* Mediterranean	*H. aurantium* North Atlantic North Pacific
	Present	*H. spinosa* South Africa Red Sea	*H. hispida* North Pacific Indo-Malayan

For fuller description see Tokioka, 1953, p. 282.

Records.—"Coasts of Hokkaido, Honsyu, Sikoku and Kyusyu but not from south coast of Sikoku and Kyusyu . . . also distributed throughout the coast of Tyosen and the coast of Shantung Peninsular in North China." (Tokioka, 1953, p. 285.)

Distribution.—In fairly shallow water in a limited area around Japan and the northern part of the Japan Sea.

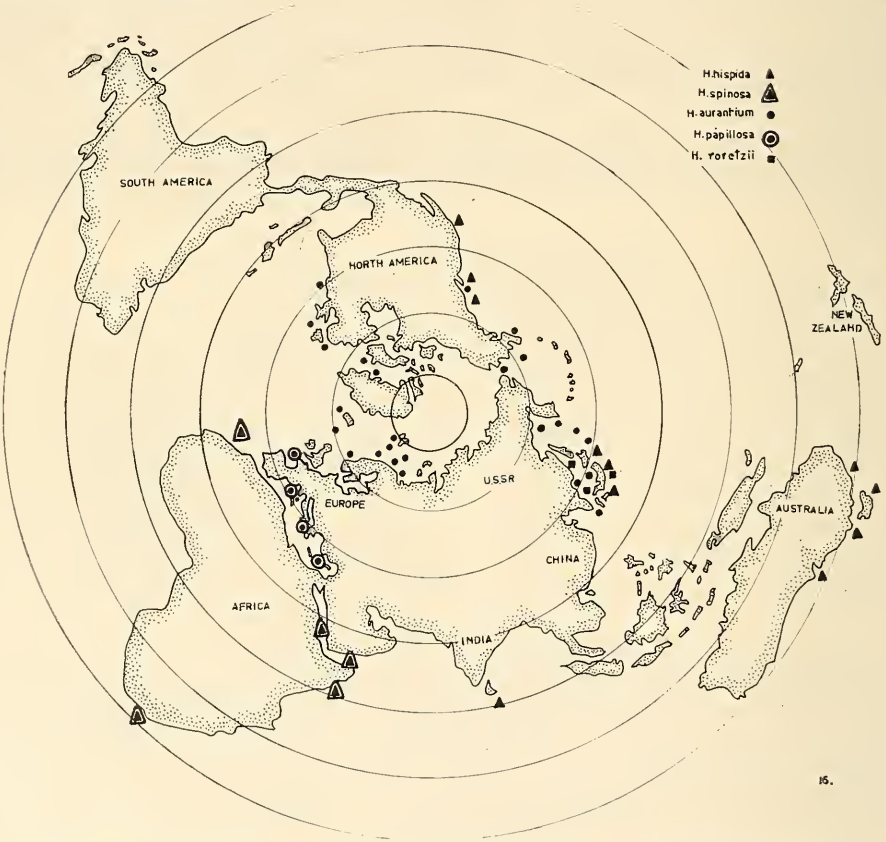
Remarks.—The species is probably related to *H. aurantium* and its distinguishing characters are largely a result of the greater development of those characters than occurs in *H. aurantium.*

Phylogeny

(Table 1, Text-fig. 3)

The four most widespread species of this genus present interesting morphological and geographical relations. From the condition in the Mediterranean species *H. papillosa* with U-shaped gonads, simple spines, and spine-bearing scales on the test, *H. aurantium* in the north Atlantic is differentiated by development of the gonads; and *H. spinosa* from South Africa and the Red Sea develops secondary branches on the test spines but retains the U-shaped gonads. This distribution of closely related species

suggest that this genus represents a relict of Tethys Sea fauna. The extension of *H. aurantium* into the north Pacific through the Bering Straits probably occurred later. However, *H. spinosa*, radiating from west of the Mediterranean southwards around Africa and north into the Red Sea could have been a Tethys component of the tropical Atlantic-West Pacific fauna. The combination of characters found in *H. hispida* may result from *H. aurantium* by the development of secondary spines, or from *H. spinosa* by the increase in the gonads. The distribution of *H. hispida* in the north Pacific and Indo-Malayan areas, as well as its morphology, is intermediate between *H. aurantium* and *H. spinosa* and its origin is probably more recent than either of the latter species.



Text-figure 3. Map showing world distribution of species of *Halocynthia*.

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References

Arnbäck-Christie-Linde, Augusta, 1928.—Northern and arctic invertebrates in the collection of the Swedish State Museum. IX. Tunicata. 3 Molgulidae and Pyuridae. *K. svenska Vetensk-Akad. Handl.*, 14(9): 1-101.

Berrill, N. J., 1929.—Studies in Tunicate development Part 1. General physiology of development of simple Ascidians. *Phil. Trans. r. Soc. (B)*, 218: 37-78.

———, 1935.—Studies in Tunicate development. III. Differential retardation and acceleration. *Phil. Trans. r. Soc. (B)*, 225: 255-326.

Bjerkan, P., 1908.—Ascidian. *In* Report of the second Norwegian Arctic Expedition, 3(14): 1-12.

Binney, W. G., 1870.—Mollusca. *In* Gould, A. A., Report on the Invertebrata of Massachusetts, 2nd edition. Boston: I-V, 1-524.

Dall, W. H., 1870.—Revision of the classification of the Mollusca of Massachusetts. *Proc. Boston Soc. nat. Hist.*, 13: 240-257.

———, 1872.—Description of sixty new forms of mollusks from the west coast of North America and the North Pacific Ocean with notes on others already described. *American Journal of Conchology*, 7: 93-160.

Drasche, R. von, 1884.—Über einige neue und weniger gekannte aussereuropäische einfache Ascidien. *Denkschr. Akad. Wiss., Wien*, 48: 369-387.

Forskal, P., 1776.—Icones rerum naturalium quas in itinere orientali depingi Curavit, Hauniae.

Gunnerus, J. E., 1765.—Vollständige Beschreibung des Seebeutels. *In* Drontheim. Gesellsh. Schrift., 3: 69.

Harant, H., 1929.—Ascidies provenant des croisières du Prince Albert Ier de Monaco. *Result. Camp scient. Prince Albert I.*, 75: 1-112.

———, and Vernières, P., 1933.—*Tuniciers Fasc. I. Ascidies. Faune Fr.*, 27: 1-101.

Hartmeyer, R., 1901.—Holosome Ascidien. *Meeresfauna*, 1: 19-63.

———, 1903.—Die Ascidien der Arktis. *Fauna arct.*, 3(2): 93-412.

———, 1904.—Ein Beitrag zur Kenntniss des Fauna des östlichen Mittelmeeres. *Zool. Anz.*, 27: 321-327.

———, 1906.—Ein Beitrag zur Kenntniss der japanischen Ascidienfauna. *Zool. Anz.*, 31: 1-30.

———, 1909-11.—Ascidien (continuation of work by Seeliger). *In* Bronn, H. G., Klassen und Ordnungen des Tier-reichs. Leipzig, 3, suppl. (89-98): 1281-1772. (Abstract, repeating lists of species by Schepotieff, A., in *Arch. Naturgesch.*, 1911, 6: 3-27.)

———, 1912.—Revision von Heller's Ascidien aus der Adria. II. Die Arten der Gattungen *Microcosmus, Cynthia, Styela, Polycarpa, Gymnocystis* und *Molgula*. *Denkschr. Akad. Wiss., Wien*, 88: 175-212.

———, 1914.—Ascidier. A conspectus of the Ascidians of Greenland. *Meddr Grønland*, 23: 1081-1117.

———, 1915.—Alder and Hancock's British Tunicaten. Ein Revision. *Mitt. zool. Mus. Berl.*, 7: 305-344.

———, 1920.—Ascidien aus dem Barentsmeer. *Wiss. Meeresunters*, New Series, 13: 125-136.

———, 1921.—Studien an westgrönlandischen Ascidien. *Meddr. Grønland*, 62: 1-137.

———, 1923.—Ascidiacea, part I. Zugleich eine Übersicht über die Arktische und boreale Ascidienfauna auf tiergeographischer Grundlage. *Ingolf-Exped.*, 2(6): 1-365.

Heller, C., 1877.—Untersuchungen über die Tunicaten des Adriatischen und Mittelmeeres. *Denkschr. Akad. Wiss. Wien*, 37: 241-275.

Herdman, W. A., 1881.—Preliminary report on the tunicata of the Challenger expedition. Cynthiidae. *Proc. r. Soc. Edinb.*, 11(3): 52-88.

———, 1882.—Report on the Tunicata collected during the voyage of H.M.S. Challenger during the years 1873-1876. Pt. 1, Ascidiae simplices. *Zool. Chall. Exp.*, 6(17): 1-296.

———, 1891.—A revised classification of the Tunicata, with definitions of the orders, sub-orders, families, sub-families and genera, and analytical keys to the species. *J. Linn. Soc. Zoology*, 23: 558-652.

———, 1899.—Description catalogue of the Tunicata in the Australian Museum. Australian Museum Sydney, Catalogue, 17: 1-139.

———, 1906.—Report on the Tunicata. Ceylon Pearl Oyster Fisheries, suppl. rept., 39(5): 295-348.

Huntsman, A. G., 1912.—Ascidians from the coasts of Canada. *Trans. r. Can. Inst.*, 9: 111-148.

———, 1912*a*.—Holosomatous ascidians from the coast of Western Canada, *Contr. Can. Biol. Fish.*, 103-185.

Jacobsohn, G.—1892.—Über d. Tunicaten d. weissen Meeres. *Trudij Leningr. Obshch. Estest.*, 23(2): 156-168.

Kiaer, J., 1893.—Oversigt over Norges Ascidiae simplices. *Forh. Vidensk. Selsk. Krist.*, 9: 1-105.

———, 1896.—Fortegnelse over Norges Ascidiae simplices. *Norske Nordhavs-Exped.*, 7(23), 3: 1-23.

Kott, Patricia, 1952.—Ascidians of Australia. 1. Stolidobranchiata and Phlebobranchiata. *Aust. J. mar. Freshwat. Res.*, 3(3): 206-333.

———, 1954.—Tunicata. *Rep. B.A.N.Z. antarct. Res. Exped.*, Series B, 1(4): 121-182.

Lacaze-Duthier, H. de, and Delage, Y., 1892.—Faune des Cynthiadées de Roscoff et côtes de Belge. *Mem. prés. div. Sav. Acad. Sci. Inst. Fr.*, (2)45: 1-319.

Linnaeus, C., 1767.—"Systema naturae". (Stockholm), 1(2): 1087, 1089, 1294, 1295, 1319.

Metcalf, M. M., 1900.—Notes on the morphology of the Tunicata. *Zool. Jb. (Anat.)*, 13: 495-602.

Michaelsen, W., 1908.—Die Pyuriden (Halocynthiiden) des Naturhistorischen Museums zu Hamburg. *Jb. Hamb. wiss. Anst.*, 25(2): 227-287.

———, 1918.—Expedition S.M. Schiff "Pola" in das Rote Meer nördliche und südliche hälfte 1895/96-1897/98 zoologische Ergebnisse. XXXII. Ascidia Ptychobranchia und Dictyobranchia des Roten Meeres. *Denkschr. Akad. Wiss., Wien*, 95: 1-120.

Millar, R. H., 1962.—Further descriptions of South African Ascidians. *Ann. S. Afr. Mus.*, 46(7): 113-221.

———, 1966.—Tunicata. Ascidiacea. Marine invertebrates of Scandinavia 1. Norges almenvitenskapelige forskningsrad D. 591 3T.

Monniot, C., 1965.—Etude Systematique et evolutive de la famille des Pyuridae (Ascidiacea). *Mem. Mus. natn. Hist. nat., Paris*, A36: 1-203.

Morse, E. S., 1871.—On the early stages of an ascidian. *Proc. Boston Soc. nat. Hist.*, 14: 351-355.

Oka, A., 1906.—Notizen über japanische Ascidien 1. *Annotnes, zool. jap.*, 6(1): 46-47.

———, 1926.—A revision of the spiniferous species of *Cynthia* (Ascidiae simplices), with a description of a new species. *Proc. imp. Acad. Japan*, 2(10): 559-561.

———, 1932.—Über eine neue stachelige *Cynthia*—Art aus Sagami Bucht. *Proc. imp. Acad. Japan*, 8(4): 131-134.

———, 1935.—Report of the biological survey of Mutsu Bay 28. Ascidiae Simplices. *Sci. Rep. Res. Insts Tohoku Univ.*, Series 4 10(3): 428-466.

Packard, A. S., 1863.—A list of animals dredged near the Caribou Island, southern Labrador during July and August, 1860. *Canadian Naturalist and Geologist*, 8: 401-429.

Pallas, P. S., 1787.—Marina varia nova et ariora. Nova Acta Academie Petropolis, 2: 229-249.

Pérès, J. M., 1958.—Ascidies de la baie de Haifa colléctees par E. Gottlieb. *Bull. Res. Coun. Israel*, 7B(3-4): 143-150.

Pratt, H. S., 1916.—Tunicata *in* "A manual of the common invertebrate animals exclusive of insects." (Chicago): 655-671.

———, 1935.—Tunicata *in* "A manual of common invertebrate animals exclusive of insects." Second edition. (Philadelphia): 735-755.

Procter, W., 1933.—Marine Fauna. Biol. Survey Mount Desert Region, Part 5, Philadelphia. Protochordates: 283-285.

Rathke, J., 1806.—Ascidians *in* Mueller, Zoologia Danica Copenhagen, 4: 31.

Redikorzev, V. V., 1916.—Tuniciers (Tunicata). *Fauna Rossi*, 1: 1-336.

Rho, Boon Jo, 1966.—Taxonomic study on the Prochordates from Korea. 1. Ascidians. *The Korean Cultural Research Institute*, 8: 209-216.

———, 1966*a*.—Taxonomic studies on the Tunicata. II. Ascidiacea and Thaliacea. *The Korean Cultural Research Institute*, 10: 361-371.

Risso, A., 1826.—"Histoire naturelle des principales productions de l'Europe meridionale." 4 (Paris).

Ritter, W. E., 1900.—Some Ascidians from Puget Sound. Collections of 1896. *Ann. N.Y. Acad. Sci.*, 12: 589-616.

———, 1907.—The ascidians collected by United States fisheries bureau steamer *Albatross* on the coast of California during the summer of 1904. *Univ. Calif. Publs Zool.*, 4: 1-52.

———, 1913.—The simple ascidians from the north-eastern Pacific in the collection of the United States National Museum. *Proc. U.S. natn. Mus.*, 45: 427-505.

———, and Forsyth, R. A., 1917.—Ascidians of the littoral zone of southern California. *Univ. Calif. Publ. Zool.*, 16: 439-512.

Roule, L., 1885.—Recherches sur les Ascidies simples des côtes de Provence (Cynthiadées). *Annls. Sci. nat.*, (6)20: 136-229.

Sars, M., 1851.—Beretning om en i Sommeren 1849, foretagen zoologiske Reise i Lofoten og Finmarken. *Nyt Mag. Naturvid.*, 6: 121-211.

Savigny, J. C., 1816.—"Mémoires sur les animaux sans vertèbres." (Paris) (2): 1-239.

Sluiter, C. P., 1905.—Tuniciers recueillis en 1904 par M. Ch. Gravier dans le Golfe de Tadjourah (Somalie française). *Mem. Soc. zool. Fr.*, 18: 5-21.

Stimpson, W., 1854.—Synopsis of the marine invertebrata of Grand Manan; or the region about the mouth of the Bay of Fundy, New Brunswick. *Smithson. Contr. Knowl.*, 6(5): 1-68.

———, 1855.—Description of some of the new marine invertebrata from the Chinese and Japanese Seas. *Proc. Acad. nat. Sci. Philad.*, 7: 375-384.
———, 1860.—A trip to Beaufort, N. Carolina. *Am. J. Sci.*, (2)29: 442-445.
Tokioka, T., 1949.—Contributions to the Japanese Ascidian Fauna II. Notes on some Ascidians collected chiefly along the coast of Kii Peninsula. *Publs Seto mar. biol. Lab.*, 1(2): 39-64.
———, 1951.—Contributions to Japanese Ascidian fauna III. The Fauna of Akkeshi Bay. XVIII Ascidia. *Contr. Seto mar. biol. Lab.*, 156: 1-22.
———, 1953.—"Ascidians of Sagami Bay (Iwanami Shoten)." (Tokyo).
———, 1959.—Contributions to Japanese Ascidian fauna XIII. Sporadic Memorandum. *Publs Seto mar. biol. Lab.*, 7(2): 223-236.
———, 1962.—Contributions to Japanese Ascidian fauna XVIII. Ascidians from Sado Island and some records from Sagami Bay. *Publs Seto mar. biol. Lab.*, 10(1): 1-20.
———, 1967.—Pacific Tunicata of the United States National Museum. *Bull. U.S. natn. Mus.*, 251: 1-242.
Traustedt, M. P. A., 1880.—Oversigt over de fra Danmark og dets nordlige Bilande kjendte Ascidiae Simplices. *Vidensk. Meddr dansk naturh. Foren. ann.* 1879-1880: 397-443.
———, 1885.—Ascidiae Simplices from det Stille Ocean. *Vidensk. meddr dansk naturh. Foren. ann.* 1884: 1-60.
Van Name, W. G., 1921.—Ascidians of the West Indian region and south eastern United States. *Bull. Am. Mus. nat. Hist.*, 44: 283-494.
———, 1945.—The North and South American Ascidians. *Bull. Am. Mus. nat. Hist.*, 84: 1-476.
Verrill, A. E., and Rathburn, R., 1879.—List of marine invertebrata from the New England Coast, distributed by the United States Comm. of fish and fisheries. *Proc. U.S. natn. Mus.*, 2: 227-232.
Wagner, N., 1885.—Die Wirbellosen des Weissen Meeres. Zoologischer Forschungsreisen am die Küste des Solowetsk Meeresbusens im die Sommermonaten d. Jahre 1877-79 u. 1882 1. Leipzig: 156.